Effect of spatial heterogeneity on natural regeneration of Manchurian ash

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Abstract: The spatial patterns of seedlings originating from natural regeneration are often heterogeneous since they are strongly influenced by microsite gradient. We supposed that the patterns of Manchurian ash (*Fraxinus mandshurica* Rupr.) seedlings, which were originated from natural seed rain, were also spatial heterogeneous in spite of relative homogeneous of planted forest. The tree seedling establishment and growth were monitored in the Forest-experimental-station of Northeast Forestry University during growing season from early May to late September in 1999. The emergence of seedlings began in middle May; but the peak was about in late May. Seedlings were counted in 635 grid cells in late June, there were about 16-30 individuals/m^2, but almost all of them died off in late September. The scale and extent of seedling heterogeneity were assessed by semivariogram and fractal dimension. The study showed that over 70% of seedling pattern was spatially autocorrelated, and that the variation caused by random factors was in less than 30%. The spatial dependent scales, both isotropy and anisotropy, were 1.95-2.92 m and 1.83-6.40 m respectively in the research stands. Our hypothesis was supported although there was difference when samples were chose at both different spatial scale and different density stands.
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Introduction

Spatial heterogeneity is an important characteristic of ecological system; it is receiving more and more attention because of its determining role in ecological pattern and process (Robertson *et al.* 1993; Cadwell *et al.* 1994; Wang *et al.* 1997,1998, Li *et al.* 1998; Wang 1999; Davie *et al.* 1998). Spatial structure created by many factors profoundly influences the dynamics, composition, and biodiversity of community (Tilman 1994). Dimension analysis in space is indispensable to explain the age-old questions about the mechanisms of plant coexistence in seemingly homogenous environment. The soil and vegetation are spatial heterogeneous at different scales in terrestrial ecosystem (Mou *et al.* 1998). Spatial heterogeneity of the physical environment may promote heterogeneity of the biotic environment, which, in turn, may differently affect the performance and fate of individuals in different spatial content.

The ecological pattern and process of regeneration are also spatial heterogeneous because many influence factors, e.g., stand structure, seed disperse and vigor trait, forest floor vegetation, litter, soil, root system, and microbian, are heterogeneous. The variation of seedling height understorey is largely caused by the spatial heterogeneity of both above- and below ground factors and their complex interactions (Kuuluvainen *et al.* 1993). The spatial patterns of light availability within stands are likely to influence regeneration patterns at stand-level (Clark *et al.* 1996).

However, fine scale environment heterogeneity within stand can also be important, e.g., the germination and growth of individual plant, which are often determined by microsite environment (Gray *et al.* 1997). Thus, the hypothesis of this study is that the patterns of emergence of seedlings, which were originated from natural regeneration, are spatial heterogeneous because there is microsite heterogeneity which is importantly potential influence to seedling establishment and growth, although there is relatively homogeneous environment in plantation. The purpose of our study was mainly to test our hypothesis, to evaluate the spatial heterogeneity scales, and to

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recognize the regeneration trait in planted forest of Manchurian ash (*Fraxinus mandshurica* Rupr.).

Methods

Site description

The study was carried out at the Forest-experimental-station of Northeast Forestry University, located in the Harbin (125°31' E, 45° 41' N), in northeast China. The area belongs to terrestrial temperature, semi-moist, and monsoon climate. Elevation is about 136-140 m. The mean yearly temperature, mean monthly temperature of July and the highest temperature are about 3.6 ℃, 22.8℃ and 36.4℃ respectively. The average annual accumulated temperature (≥10℃) is about 2 757℃. Frost-free period is 130-140 d. In winter season, mean monthly temperature of January and the lowest temperature are –19.4℃ and -38.1℃. The total yearly rainfall is about 600 mm, more than 80% is concentrated among June, July, and August (Mu *et al.* 1991). The soils are black earth and chernozem earth.

The vegetation in this area was primarily grass with a few of elm (*Ulmus spp.*) trees, but it has been replaced by plantation now. The study stand, planted in 1954, was pure Manchurian ash. There are two stand densities, one (S_1) is 700 individual/hm^2, and another (S_2) is 1 200 individuals/hm^2. The forest floor vegetation is mainly herbaceous.

Field methods

At low-density stand (S_1), three quadrat plots, one quadrat (Q_1) for 30 m x 30 m and two quadrat (Q_2, Q_3) for 10 m x 10 m, were set up for the purpose of comparing spatial variation of natural regeneration with different spatial sample scales. To found difference of heterogeneity at different density stands, one plot (Q_4) of 10 m x 10 m was established in relatively highly density stand (S_2).

There are 225 removable grids (2 m x 2 m) in plot Q_1, and 100 removable grids (1 m x 1 m) in plots (Q_2, Q_3, and Q_4) respectively. The seedlings of natural regeneration were counted in each grid cell (30 cmx30 cm), which were temporarily established in center of each grid cell after the peak of seedling emergence in late June. To measure height growth of seedlings, 50 small plots randomly located, in size of 30 cm x 30 cm, were established in plot Q_1, and 20 small plots in Q_2, Q_3, and Q_4 respectively.

To monitor emergence of seedlings, which were originated from natural seed rain, two-observation plots (1 m^2) randomly located were set up in two stands prior to seedling germination. The plots were surveyed every day from early May to middle May. After then we made periodic surveys every week. In late June, when new germinants were rare, the plots were surveyed every 3 or 4 weeks until late August. These observation plots were revisited in middle and late September to observe seedlings survival.

Date analysis

All data were first examined using descriptive statistics. Seedling abundance (mean density of first year seedlings), frequency distribution of population, coefficient of variation, and skewness were evaluated for each plot individually. The height of seedling was also examined at two different density stands.

The variation of spatial heterogeneity can be decomposed into two parts: random variation and autocorrelated variation. This variation or spatial heterogeneity of seedlings pattern can be evaluated by semivariograms (Li *et al.* 1999; Wang *et al.* 1999). Spatial statistics were computed using GS+software for seedling abundance. Data were highly skewed, and were lognormally transformed (ln(z+1)) prior to analysis in order to better normalize probability distribution. After lognormal transformation the skewness of data was modified from 1.77-1.97 to 0.24-0.58. In a semivariogram, semivariance was plotted on the y-axis against lag distance on the x-axis. Semivariance was calculated and then models were fitted via least-squares analysis. When calculating anisotropic semivariance, the principal axis is 0 , offset tolerance is 22.5°, and offset is 0°, 45°, 90°, and 135°.

For the data of Q_1, semivariance pairs were grouped into 9 separation distance classes between 0 to 32 m, the separation distance (uniform interval) between each class was 3.17 m, and active lag distance was 31.68 m. For variogram models of Q_1 the semivariance data were fit to spherical models. The semivariance pairs of Q_2, Q_3, and Q_4 were grouped into 8 or 9 separation distance classes between 0 and 11 m, the separation distance between each class was 1 m, and active lag distance for 9.18-10.18 m. The exponential or spherical models were fitted. However, some groups of semivariance data there are no fit models.

The important parameters, including nugget variance (C_0), structure variance (C), sill (C+C_0), rang (A), fractal dimension (D), were evaluated by models. The proportion of model sample variance explained by structure variance was used as a normalized measurement of spatial dependence for a particular variate. The proportion ($C/[C_0+C]$) approaches 1, meaning high spatial dependence. While the proportion approaches 0, meaning low spatial dependence, or high measurement error, or spatial dependence occurring mainly at small scale (Robertson *et al.* 1997).

Results

The germination of seedling of natural regeneration started in mid-May when the temperature was about 7-16℃; while a large amount of seedlings germinated in late May when the temperature was about 6-20℃. After mid-June, the new germinates were rare. The pattern of seedling population was assemblage distribution, according to variance analysis of data, because the proportion of sample variance against mean (s^2/x) are over 1 (1.93-3.50), (Wang 1999).

In stand S_1, the mean height of first year seedling was 6.9 cm, the densities ranged from 0 to 122 individuals/m^2, mean seedling density was 16 individuals /m^2, and its coefficient of variance ranged from 114%-118%. The frequency distribution of seedling population was highly skewed (Table 1, Fig.1). Of total 425 grid cells, over 35% of grid cells had no seedlings, 25% of grid cells was one seedling in a grid cell.

In stand S_2, regeneration seedling densities ranged from 0 to 166 individuals/m^2, mean density was 30 individuals /m^2, and coefficient of variation is 114%. The frequency distribution was also highly skewed. 22% of grid cells were no seedlings, and 40% of grid cells were 1 or 2 seedlings.

Table 1. The result of descriptive statistics analysis and variance analysis

Quadrat	Mean Value	Standard deviation	Sample variance	Min. value	Max. value	Number	Skews (se)	Transformed Skewness (se)
Q1	1.507	1.783	3.180	0.0	11.0	225	1.77(0.16)	0.37(0.16)
Q 2	1.500	2.018	4.071	0.0	10.0	100	1.97(0.24)	0.58(0.24)
Q 3	1.360	1.624	2.637	0.0	8.0	100	1.75(0.24)	0.40(0.24)
Q 4	2.690	3.074	9.448	0.0	15.0	100	1.91(0.24)	0.24(0.24)

Notes: Mean value: mean seedling densities in grid cell

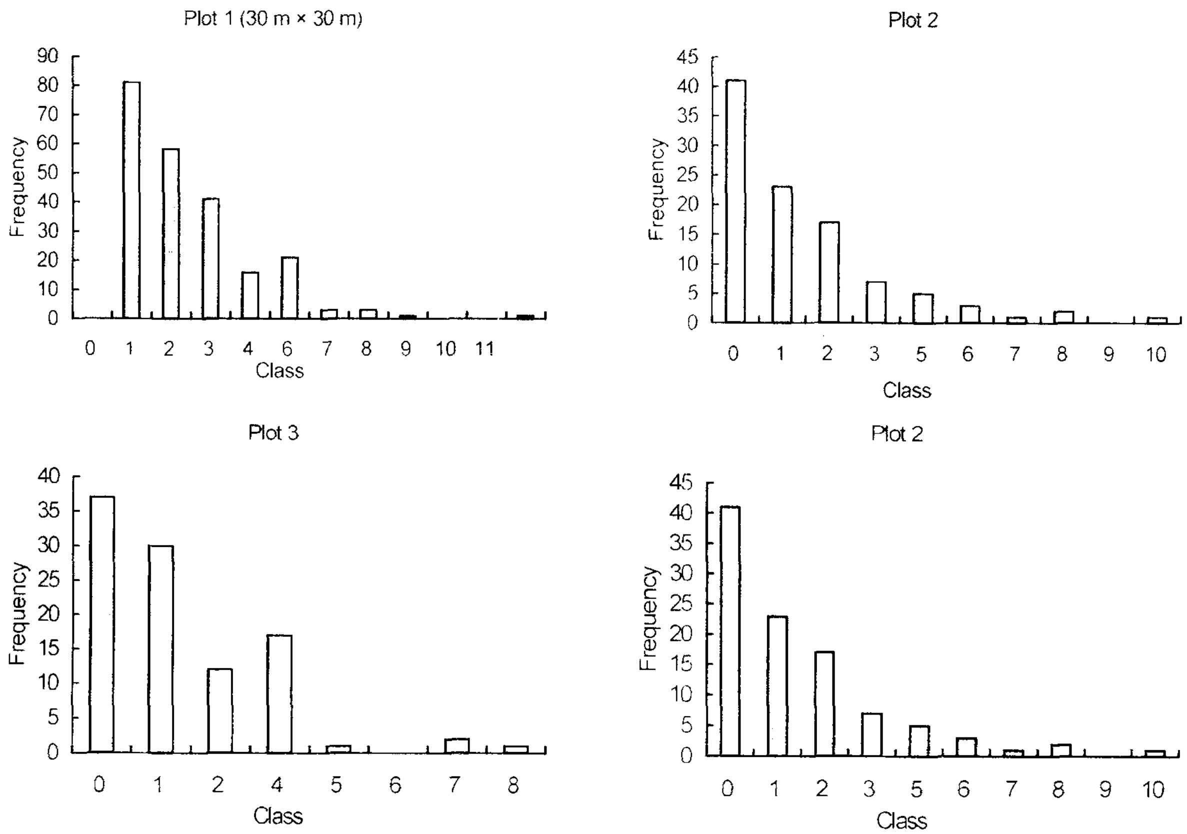

Fig. 1. Frequency distribution of seedling population of Manchurian ash

Spatial patterns of seedlings were examined at tow different levels: (1) different scales within a stand (Q_1, Q_2, and Q_3 in S_1); (2) stand level (Q_4 in S_2). Semivariogram parameters, both isotropy and ani-

sotropy, were given in Table 2, fractal dimensions in Table 3 and the fitting models also in the Table 4. For Q_1, spherical models were fitted, while for Q_2 exponential models were chose since their R^2 were higher than other models. However, for Q_3 and Q_4, there were no clear models in isotropic semivariogram or model fits were poor since lower R^2, indicating that random factors or smaller scale heterogeneity were important.

In stand S_1, no strong difference of total sample variance (sill) was found among different sample scales within a stand, indicating a similar trend of total variation. The sill (C_0+C) values of models can give best expression of sample variance because the RSS (residual standard square) is lower (0.000-0.056). Seeding patterns were spatially autocorrelated at scales of 1.95-2.92 m in isotropic heterogeneity, and 1.83-6.40 m in anisotropic heterogeneity. Over 70% of sample variance was spatially dependent at these scales.

Table 2. Semivariogram model parameters for seedling of natural regeneration

Quadrat		Models	Nugget (C_0)	Sill (C_0+C)	Range (A)	Effective range	Proportion (C/C_0+C)	R^2	RSS
Q_1	Isotropy	Spherical	0.109	0.400	2.92	2.92	0.727	0.366	0.000
	Anisotropy	Spherical	0.001	0.470	3.28	3.28	0.998	0.295	0.039
					4.07	4.07			
Q_2	Isotropy	Exponential	0.130	0.437	0.65	1.95	0.702	0.644	0.019
	Anisotropy	Exponential	0.001	0.563	2.14	6.40	0.998	0.288	0.056
					2.14	6.40			
Q_3	Isotropy	Spherical	0.087	0.374	1.00	1.00	0.768	0.000	0.002
	Anisotropy	Spherical	0.001	0.479	1.83	1.83	0.998	0.247	0.062
					1.96	1.96			
Q_4	Isotropy	Spherical	0.139	0.556	1.00	1.00	0.750	0.000	0.002
	Anisotropy	Exponential	0.001	0.668	1.04	3.12	0.999	0.231	0.099
					1.14	3.42			

Notes: Nugget variance (C_0): Randomly part of spatial heterogeneity variance; Sill: (C_0+C): model sample variance or total variance of spatial heterogeneity; Range (A): distance over which spatial dependence part of spatial heterogeneity is expressed; Proportion ($C/[C_0+C]$): relative structural variance or autocorrelated part of spatial heterogeneity; Spherical model: $r(h)=C_0+C(3/2[h/a]-1/2[h^3/a^3])$ $0< h \leqslant a$, $r(h)=0$ $h=0$, $r(h)=C_0+C$ $h>0$; Exponential model: $r(h)=C_0+C(1-e^{-(h/a)})$ $h>0$, $r(h)=0$ $h=0$.

Table 3. Fractal dimension analysis

Quadrats		Isotropy	Anisotropy 0°	45°	90°	135°
Q_1	D	1.993	1.983	1.990	1.970	1.997
	se	0.978	0.902	2.359	0.634	5.033
	R^2	0.372	0.408	0.032	0.580	0.022
	Number	9	9	9	9	9
	C_V %	49.07	45.49	118.54	32.18	252.03
Q_2	D	1.959	1.972	1.977	1.959	1.933
	se	0.389	1.363	1.956	1.490	0.835
	R^2	0.809	0.259	0.170	0.224	0.517
	Number	8	8	7	8	7
	C_V %	19.86	69.12	98.97	76.06	43.20
Q_3	D	1.979	1.965	1.969	1.981	1.938
	se	0.894	1.386	1.762	2.793	0.761
	R^2	0.412	0.233	0.172	0.067	0.519
	Number	9	9	9	9	8
	C_V %	45.17	70.53	89.49	140.99	39.27
Q_4	D	1.993	1.971	1.968	1.983	1.935
	se	1.974	1.425	1.296	3.090	0.447
	R^2	0.127	0.215	0.278	0.056	0.757
	Number	9	9	8	9	8
	C_V %	99.05	72.29	65.85	155.82	23.10

Notes: The principal axis is 0 °; The direction of 0 °and 90 °coincides with the direction of row of trees of overstory; D-- Fractal dimension.

In stand S_2, the total sample variance (0.556-0.668) was slightly higher than S_1 (0.374-0.563), showing a

higher heterogeneity. But the model fits were poor, although the anisotropic semivariogram was poorly fitted by exponential model, meaning that random pattern or smaller scales (lower than our sample scales) heterogeneity was probably important in this stand.

Fractal dimension was examined at different directions of seedling distribution. And a significant difference was demonstrated, showing an obviously anisotropic seedling pattern. In stand S_1, fractal dimension (D) ranged from 1.938-1.997, coefficient of variance of fractal dimension ranged from 19.86% (in Q_2) to 252% (in Q_1). In stand S_2, coefficient of variance of fractal dimension (99%) is higher than stand S_1 (19%-49%) in isotropic semivariogram.

Discussion

Seedling emergence and distribution

This study indicated that the emergence time of natural regeneration seedling of Manchurian ash was varied during the growing seasons and that the pattern of seedlings was apparently assemblage distribution in tow stands. Germination, which began in middle May, was much great in late May. A few of seeds still emerged after middle June. The seedling root was about 3-4 cm long when two cotyledons were raised above the forest floor. In the end of growing season the heights of first year seedlings was 7-8 cm, roots for also 7-8 cm long, involving 18-20 branch roots. There were about 4-6 leaves in a seedling; its cotyledons were wilted along with leaves at same time or later in middle or late September. Seedling densities varied dramatically, ranging from 0/m^2-167 individuals/m^2, after the germination peak. Many seedlings can be obviously observed in microsite areas where the soil was loosed, and less seedlings to be found in other microsite areas where the cover of stand floor vegetation (mainly herbaceous) was higher although in those areas many seeds buried in seed bank could be found. Herbaceous vegetation, which has great density roots in the layer of topsoil, may locally deplete soil moisture and nutrients, which inhibited natural regeneration seedling establishment.

Spatial heterogeneity of seedlings

This study's major objectives is to determine whether patterns of natural regeneration seedlings of Manchurian ash were spatial heterogeneous in relatively homogeneous planted forest, to examine autocorrelated scales of spatial heterogeneity and to compare the differences both density stands and different sample scales. The results showed that the patterns of natural regeneration seedlings were spatial heterogeneous although there were difference at both different stand densities and different scales. The autocorrelated scales of spatial pattern ranged from 1.95 m to 2.92 m in isotropy and form 1.96 to 6.40 m in anisotropy in research stands. The patterns of seedlings were spatial dependent with those scales. Over 70% of spatial heterogeneity of seedling pattern was spatial autocorrelated variation, less than 30% of which might be caused by random factors. This means that there are stronger spatial patterns of regeneration seedlings.

Seedling without strong.root system was limited to locally microsite for its nutrient uptaking and resource using, resulting that the establishment of natural regeneration seedlings appeared to be quite sensitive to microsite heterogeneity (Liu *et al.* 1994). The patterns of seed bank were often of spatial heterogeneity (Matlack *et al.* 1990). Seed germination and the process of seedling establishment may be strongly affected by locally inhabited environment. A certain microsite may be a favorable environment for emergence of seedlings, this results spatial heterogeneous patterna for natural regeneration seedlings.

Within a stand, the difference of spatial heterogeneity was found at different sample scales. For plot of Q_3, the model fits were poor with semivariogram analysis, potentially indicating a random spatial pattern in this plot. The difference of spatial heterogeneity between two density stands was apparent. For higher density stand (more adult trees in a stand), the total sample variance was higher than that of lower density stand (much less adult trees in a stand). But the spatial heterogeneity mainly attributed to random factors, or potentially meaning that spatial dependence may be in smaller scales (smaller than our sample scales).

For stand S_1 the adult tree density was lower, meanwhile the seedlings density of natural regeneration was also lower (16 individuals/m^2 on average). Within stand S_2 the adult tree density was higher, and its seedlings density of natural regeneration was also higher (30 individuals/m^2 on average). This difference in seedling density was likely to be influenced by a complex set of interacting ecological factors. The pattern of stand-level regeneration may be in consequence of spatial pattern of light availability (Clark *et al.* 1996). But in this study, in stand with less light and herbaceous plant, there were more seedlings. Understory herbaceous plant may be an important competitor that inhibited the process of seedling establishment. However, in this study the positive effects of light on seeding establishment may be compromised by the simultaneous negative effects of herbal plant growing. There were few of seedlings surviving over a year in spite of so many seedlings emergence in early growing season. A few of two or three years old seedlings were found in high light

microsite area. The patterns and causes of those seedlings, the mutual relation between seedling emergence as well as seedling survival need further research.

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